Species on the move: Stowaways and contaminants cause the greatest economic impacts

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Abstract

Introduction pathways play a pivotal role in the success of Invasive Alien Species (IAS) – the subset of alien species that have a negative environmental and/or socio-economic impact. Pathways refer to the fundamental mechanism that leads to the introduction of a species outside of its native range – marking the beginning of all alien species invasions. Increased knowledge of pathways is essential to help reduce the flow and impacts of IAS and ultimately improve their management. Here we use the *InvaCost* database, a comprehensive repository on the global monetary impacts of invasive alien species, combined with the CBD hierarchical classification of introduction pathways to address four key questions: (i) Are particular IAS introduction pathways economically impactful? (ii) How are costs taxonomically and spatially distributed across pathways? (iii) Are there differences in costs between species introduced intentionally and unintentionally? and (iv) is there a relationship between the number of possible introduction pathways of IAS and their costs? We found first that both the total and average cost of species introduced through ‘Stowaways’ (US\$144.9bn; US\$89.4m) and ‘Contaminants’ pathways (US\$99.3bn; US\$158.0m) were more costly than species introduced primarily through ‘Escape’ (US\$87.4bn; US\$25.4m) and ‘Release’ (US\$64.2bn; US\$16.4m). Second, insects drove the costs of unintentional introductions whilst mammals drove the costs of intentional introductions; ‘Stowaways’ had the highest costs in Asia, Central America, North America and Diverse/Unspecified regions, whilst Antarctic-Subantarctic and Oceania incurred the greatest costs from species introduced through ‘Release’. Third, the cost of species introduced unintentionally is more than double the cost of species introduced intentionally (\$192bn vs. \$90bn). Equally, species introduced unintentionally cost more on average than species introduced intentionally in terms of damage, management, and mixed costs. Finally, the total and average cost of IAS was not related to their number of introduction pathways. Our findings provide important material for the targeting of priority pathways - something that will be critical in prioritising limited management budgets to combat the current acceleration of species invasions.

Introduction

All alien species invasions begin with the intentional or accidental transportation of individuals or propagules by humans outside of their historical biogeographic boundaries (Blackburn et al., 2011; Lehan et al., 2013, Essl et al. 2015). Pathways refer to the fundamental mechanism that leads to the introduction of a species outside of its native range. Consequently, pathways play a pivotal role in the success of Invasive Alien Species (IAS) – the subset of alien species that have a negative environmental and/or socio-economic impact – as they influence the number, frequency and geographic range of propagules dispersed (Pyšek et al., 2020). Increased knowledge of pathways is crucial to help reduce the flow and impacts of IAS (Leung et al. 2002, Essl et al. 2015) and ultimately improve their management (Simberloff and Rejmanek 2011, Novoa et al. 2020). In recent years, research and policy have focused on identifying and classifying introduction pathways and prioritising which pathways to manage in order to prevent biological invasions. This was illustrated by the Strategic Plan for Biodiversity 2011–2020

(Target 9; Convention on Biological Diversity 2012; <https://www.cbd.int/sp/targets/rationale/target-9/>) in which parties aspired that *'by 2020, invasive alien species and pathways are identified and prioritized'*.

Many pathways of introduction (henceforth, 'pathways') have already been identified through assessments at regional levels and across ecosystems. These assessments help advance our understanding of IAS flows and support the development of policy tools (Hulme et al., 2008; Essl et al., 2015; Katsanevakis et al., 2013; Pyšek et al., 2011, Nuñez et al., 2015; García-Berthou et al., 2005, Pergl et al., 2017). Global databases of IAS such as the IUCN's Global Invasive Species Database (GISD, www.iucngisd.org) and the CABI Invasive Species Compendium (CABI ISC, www.cabi.org/isc) list between 34 and 80 different pathways through which alien species can invade new locations. Examples of pathways include horticulture (e.g. purple loosestrife, *Lythrum salicaria*), agriculture (e.g. cane toad, *Rhinella marina*), pet trade (e.g. Burmese python, *Python bivittatus*) and stowaway transport (e.g. zebra mussel, *Dreissena polymorpha*). Such lists are neither exhaustive nor static; as societies evolve and economic activities continue to grow, more introduction pathways are expected to emerge. To facilitate comparative studies on pathways, Hulme et al. (2008) developed a framework using a hierarchical classification of pathways, subsequently adopted by the Convention on Biological Diversity (CBD, 2014). The hierarchical approach encompasses three levels; the first level is three broad mechanisms through which species may arrive to a new location: movement of commodities, arrival of a transport vector, and/or natural spread from a neighbouring region. These three mechanisms then encompass six primary introduction pathways (Hulme et al., 2008): 'Release' (intentional introduction as a commodity for release), 'Escape' (intentional introduction as a commodity but unintentional escape), 'Contaminant' (unintentional introduction with a specific commodity), 'Stowaway' (unintentional introduction attached to or within a transport vector), 'Corridor' (unintentional introduction via human infrastructures linking previously unconnected regions), and 'Unaided' movement (unintentional introduction through natural dispersal of alien species across political borders). These six pathways are further divided into 44 subcategories, covering all possible ways of introduction (Fig. 1).

Prioritizing the management of high-risk pathways is necessary to achieve cost-effective management of IAS, essentially by preventing the introduction of additional harmful alien species (McGeoch et al., 2016). IAS can generate substantial costs in terms of damage to ecosystems, impacts on human well-being and expenditures on management (Diagne et al., in press). At the same time, there is evidence that investing in the prevention of IAS introduction (proactive management) is less costly - and likely more efficient - compared to allocating resources and funds to reactive management once they establish and become invasive (Leung et al., 2002).

Pathways can be prioritized by urgency using (i) the number of IAS introduced per pathway and/or (ii) an assessment of the impact caused by species introduced following specific pathways (Essl et al., 2015; McGeoch et al., 2016), and these two prioritizations can lead to conflicting results. On the one hand, studies that investigated the number of species per pathway have found that movement of commodities was responsible for the most introductions. Indeed, 'Escape' is identified as the most prevalent pathway for IAS, predominantly through horticulture trade (McGrannachan, et al., 2020; Saul et al., 2017; Turbelin

et al., 2017). On the other hand, previous studies showed that invaders associated with a high number of introduction pathways are more likely to have an ecological impact in newly invaded sites (Pergl et al., 2017; Saul et al., 2017). Particularly for plants, both the number and types of pathways can influence invasion success and the likelihood of impact (Pysek et al. 2011; Pergl et al., 2017). Plants introduced through 'Release', 'Corridor' and 'Unaided' pathways are more likely to have an ecological impact than when introduced as 'Contaminants' (Pergl et al., 2017) and to successfully establish and be accepted in society when grown as animal food or for environmental uses (van Kleunen et al., 2020).

Whilst a number of publications have examined the links between ecological impacts and pathways of IAS, there are currently no studies assessing relationships between introduction pathways and economic impacts of IAS. Economic impact is a very useful metric of the impact of IAS, as it can be quantitative, and if costs are standardized, they can be compiled across regions or taxa and compared between pathways. A better understanding of the economic costs of invasions is also a key way to raise global awareness about IAS, optimise transboundary legislation and help the prioritisation of management actions (Diagne et al. 2020a).

In this paper, we investigate introduction pathways of economically-harmful IAS using the most up-to-date compilation of monetary cost information on IAS - the *InvaCost* database (Diagne et al. 2020b) and the CBD hierarchical classification of introduction pathways (CBD, 2014; Hulme et al. 2008). Specifically, we address the following questions: (i) Are particular introduction pathways economically impactful? (ii) How are costs taxonomically and spatially distributed across pathways? (iii) Are there differences in costs between species introduced intentionally and unintentionally? and (iv) is there a relationship between the number of possible introduction pathways of IAS and their costs?

Methods

Cost data collection and filtering

To assess the economic impact of IAS over the last 50 years (1970-2020), we relied on cost data recorded in the latest version of *InvaCost* (version 3.0, openly available at <https://doi.org/10.6084/m9.figshare.12668570>), which is the most complete and up-to-date global dataset of the reported economic costs attributable to biological invasions (Diagne et al. 2020b). *InvaCost* has been built by a combination of both systematic literature searches (e.g., specific search strings used in Web of Science and Google Scholar) and direct solicitations (e.g., stakeholders, scientific experts) to gather any cost information available in written documents in more than 10 languages. After ensuring relevance of each document collected, cost information was collated, standardised to a common and up-to-date currency in the database (i.e. 2017 US dollars), and finally classified into categories using a range of descriptive fields that allow a multidimensional description of the cost estimates collated (complete description and details on these descriptive fields are available at <https://doi.org/10.6084/m9.figshare.12668570>). This updatable and publicly available resource now

contains 9,823 cost entries (as of January 2021), therefore providing an essential basis for worldwide research and policymaking targeting IAS (Diagne et al. 2020a, 2020b).

We used successive filters from the *InvaCost* database to identify relevant cost entries for our analysis and obtain a conservative and realistic estimate of costs. First, we extracted costs empirically “observed” in the invaded environment, and left out all “potential” costs (not yet actually realised but rather expected and/or predicted over time within or beyond their actual distribution area: *Implementation* column). Second, we then retained costs classified as “high” reliability – therefore discarding “low” reliability costs – (*Method_reliability* column), thereby keeping only cost estimates either provided by officially pre-assessed documents (peer-reviewed articles and official reports) or associated with an estimation methodology that was deemed reproducible when building the database (Diagne et al., 2020b). Lastly, we focused on cost estimates exclusively attributed to individual species, therefore multi-species costs or genus-level costs were removed (e.g. when the estimate in the *Species* column included “sp.” or “spp.” or was simultaneously associated with several species without any possibility to disentangle specific contribution of each taxon to the overall cost). Following these filtering steps, our dataset (hereafter called *filtered_subset*) contained 5,627 entries (**Supplementary Material 1**). All costs are presented in USD 2017 values following cost standardisation procedures described in Diagne et al. (2020b). Finally, we extracted the list of individual species with recorded costs to assign pathways. After checking for discrepancies in species names (i.e., where entries for the same species have different scientific names we opted for the internationally preferred Scientific Name as described in CABI), the number of individual species with cost records amounted to 515.

Collection and compilation of pathway information

Pathways were categorised using the pathway classification framework developed by Hulme et al. (2008) and adopted by the Convention on Biological Diversity (CBD, 2014). This framework uses a hierarchical approach in which alien species may arrive in a new location through three broad mechanisms (i.e. movement of a commodity, arrival of a transport vector, or spread from a neighbouring region), 6 main pathways (i.e. release, escape, contaminant, stowaway, corridor, and unaided) and 44 pathway subcategories (e.g. ornamental, aquaculture, seed contaminant, etc.) (**Figure 1**). Pathway mechanisms, categories and subcategories are defined in **Supplementary Material 2**. We compiled pathway data for each of the 515 species with reported economic costs in our *filtered_subset* (Supplementary Material 3, which contains all columns hereafter mentioned) mainly using information from CABI ISC (www.cabi.org/isc/) and the GISD (<http://www.iucngisd.org/gisd/>); when the information needed was not available in one of these repositories, we opportunistically extended our searches to other databases on biological invasions (e.g. the Galapagos Species Checklist), as well as in targeted published literature. Pathway descriptions provided in databases or publications, which do not always match the CBD pathway sub-categories, were added to a column named *pathway_description* and the source (CABI ISC, GISD, etc.) to a column named *Source*. The pathway description was matched using the CBD guidance for interpretation of the categories on introduction pathways (Harrower et al., 2018) to one of the 44 CBD subcategories (*CBD_subcategory* column), one of the 6 corresponding CBD pathway categories

(*CBD_pathway* column) and one of the 3 broad CBD pathway mechanisms (*CBD_mechanism* column), respectively.

As stated by the CBD: *“Moreover, the pathway category assigned to a species is typically the pathway(s) that relates directly to the species being introduced. However, the introduction of a species may also be indirectly dependent on another pathway, particularly when the species is contaminant of another species or product. Although these dependent pathways are not directly related to the species they play a part in understanding the process of introduction and are, therefore, important for decision-making and particularly in relation to prevention through management of pathways. As these dependent pathways are important they should be recorded, but as they are not directly related to the species it is important they are not confused with the pathway information that directly relates to the species.”* As such, we incorporated a *Direct_or_Indirect* column to highlight pathway dependency, and to indicate whether the pathway was related directly to the species being introduced (*Direct*) or when the pathway was related to a species or product that the species being introduced is dependent upon (*Indirect*).

Finally, as IAS can have multiple pathways of introduction, we determined the most important pathways for each species by classifying each pathway as ‘primary’ or ‘secondary’ (*Primary_or_Secondary* column) based on the above-mentioned source information. A pathway was categorised as ‘primary’ when it was clearly recognised as one of the most important in the source document, i.e. likely leading to successful long-distance introductions as a result of increased propagule pressure (number, frequency and range of propagules) or by facilitating spread or escape. Conversely, a pathway was categorised as ‘secondary’ when it was less likely to lead to the successful establishment of a species, generally due to either low propagule pressure (i.e. low number of introduction events, low number of individuals per introduction event) or due to it mainly promoting short distance/local dispersal of the species. We classified pathways as ‘secondary’ only when the information provided in databases or publications enabled us to identify primary pathways. Otherwise, pathways were classified as primary. It was thus possible for a species to have more than one primary pathway.

There is a level of inherent uncertainty associated with the compilation of data collated in large-scale databases. We minimized the level of uncertainty associated with pathway-related data input in two ways depending on the source of uncertainty. First, data collation and merging between different data resources may be a source of potential confusion and errors. Therefore, we checked for (and then systematically corrected) obvious mistakes in pathway assignment using our expert judgement. Second, uncertainty may also arise from the varying quality of the source attributing a pathway to a particular species. Indeed, pathways may be assigned based on (i) information from the peer-reviewed literature – providing evidence of transport of a species from one region to another, (ii) indirect evidence of pathway use reported in grey literature (e.g. individuals found near botanic gardens), and (iii) assumptions/deductions made from similar species’ introduction pathways (Harrower et al., 2018).

Data processing and analysis

We used the *expandYearlyCosts()* function from the ‘invacost’ package version 0.3-4 (Leroy et al., 2020) in R version 4.0.3 (R Core Team 2020) to ensure that each cost entry - which could correspond to either a single or a multi-year estimate - was consistently recorded on an annual basis for the amount of years that the cost was incurred. The period of cost occurrence was calculated as the difference between the first year (*Probable_starting_year_adjusted* column) and the ending year (*Probable_ending_year_adjusted* column) of the cost record. The expanded version of our *filtered_subset* contained 10,183 cost entries (hereafter called *expanded_subset*). Finally, we used the R package dplyr (version 1.0.2.) (Wickham et al., 2020) to merge the *expanded_subset* with the pathways dataset (**Supplementary Material 3**) and generate our *final dataset*, available in **Supplementary Material 4**. Our *final dataset* contained 52,454 entries covering over 107 countries.

To estimate the economic impact (or cost) of invasive species for the period 1970-2020, we calculated the total cumulative costs over time observed between 1970 and 2020, by summing all cost estimates provided in the *Cost_estimate_per_year_2017_USD_exchange_rate* column of our *final dataset*. We also calculated the average cost of species, by averaging the mean costs calculated for every species according to each reported pathway (**Supplementary Material 5**). We used the Kruskal-Wallis rank sum test to compare the average and total cost per species across pathway categories and subcategories. Multiple comparisons were further carried out with pairwise Wilcoxon rank sum tests (95% family-wise confidence level).

Total and average costs were provided for the different taxa recorded in our final dataset. IAS were classified into 13 broad “organism types” based on information from the *Kingdom*, *Phylum*, and *Class* columns: amphibian, arthropods, bird, decapod, fish, fungi, insect, mammal, mollusc, plant, reptile, animalia diverse and other organisms. “Animalia diverse” include species from the *Kingdom* Animalia that are not listed in the above animal categories (e.g. species of the class Ascidiacea or phylum Nematoda). The category “other organisms” is made up of all organisms not included in the aforementioned categories (e.g. species with *Kingdom* column entries Bacteria, Virus, Chromista).

To examine potential differences in damage and management costs between species introduced intentionally and unintentionally, and across pathways, we used information from the *Type_of_cost_merged* column in our *final dataset*, which classifies the cost estimates as “damage” (i.e. economic losses due to direct and/or indirect impacts of invaders, such as yield losses, damage repair, etc.), “management” (i.e. economic resources allocated to actions related to the prevention, management and control of alien species) or “mixed” (i.e. when costs incorporate both ‘damage’ and ‘management’ elements) costs.

The number of introduction pathways per species was calculated by summing the number of pathways (*CBD_pathway* column) and pathways subcategory (*CBD_subcategory* column) for each species.

We used ggplot2 (v.3.3.2, Wickham 2011) R package to generate all figures.

Results

Our final dataset contained cost data for 515 individual species. Pathway information was available for 412 species (80%), whilst 106 species (20%) currently have unknown pathways.

Are particular IAS introduction pathways economically impactful?

Considering only primary pathways, we found that 'Stowaways' and 'Contaminants' were globally associated with the highest monetary losses and expenditures. This pattern was consistent when considering both the *(i)* total costs (Table 1; Fig. 2a) over the last 50 years (1970–2020) as well as *(ii)* the average cost per species (KW test = 72.391; $p < 0.001$; Fig. 2b). IAS introduced via 'Stowaways' (\$144.9bn) and 'Contaminants' (\$99.3bn) exhibited higher costs than those introduced through 'Escape' (\$87.4bn), 'Release' (\$64.2bn) and other pathways (i.e. less than \$1bn). Equally, species introduced as 'Contaminants' (\$158.0m; median: \$1.9m) and 'Stowaways' (\$89.4m; median: \$1.8m) were more likely to cost more than species introduced intentionally through 'Release' (\$16.4 million; median: \$0.08m) or 'Escape' (\$25.4m; median: \$0.06m). This pattern was observed despite the larger number of species found to be introduced through 'Escape' (217) than through 'Contaminants' (126) or 'Stowaways' (84) pathways. This finding remains true even when including secondary pathways in the analyses (KW test = 41.546; $p < 0.001$; see **Supplementary Material 6** for details on Wilcoxon pairwise comparisons).

Table 1

Cost of invasive alien species by pathway of introduction. The total cost is the sum of all costs attributed to invasive alien species for each pathway category from 1970 to 2020 and the average cost is the average cost of a species in a given pathway.

Invasive alien species cost per pathway (direct and primary pathways)				
CBD Mechanism	Pathway	# Species	Average cost million (2017 USD)	Total cost million (2017 USD)
VECTOR	Stowaway	84	\$89	\$144,918
Movement of COMMODITY	Contaminant	126	\$158	\$99,327
Movement of COMMODITY	Escape	217	\$25	\$87,371
Movement of COMMODITY	Release	109	\$16	\$64,183
SPREAD	Unaided	6	\$12	\$760
SPREAD	Corridor	6	\$0.2	\$35
Invasive alien species cost per pathway (direct, primary and secondary pathways)				
CBD Mechanism	Pathway	# Species	Average cost million (2017 USD)	Total cost million (2017 USD)
VECTOR	Stowaway	157	\$69	\$179,143
Movement of COMMODITY	Contaminant	205	\$101	\$161,069
Movement of COMMODITY	Escape	235	\$23	\$98,360
Movement of COMMODITY	Release	155	\$13	\$70,823
SPREAD	Unaided	164	\$57	\$32,623
SPREAD	Corridor	27	\$11	\$4,028
Unknown	Unknown	106	\$71	\$15,307

'Corridor' and 'Unaided', were generally classified as secondary pathways; nevertheless for a relatively small amount of species (n = 12) (e.g. *Salvinia molesta*, *Gymnocephalus cernuus*) these were also classified as the primary means of dispersal. The total costs incurred as a result of species introduced through 'Corridors' and 'Unaided' pathways were the lowest, costing \$0.04bn and \$0.8bn between 1970 and 2020, respectively. However, the average cost of species spread through 'Corridor' was \$0.2m and 'Unaided' \$33.4m (median species costs: \$0.1 and \$5.7m).

The three direct, primary pathway subcategories with the highest average species cost were 'Machinery & equipment', 'Fishing equipment' and 'Food contaminant' whilst the three pathway subcategories with the lowest average species cost were 'Fishery in the wild', 'Research', and 'Agriculture' (see Fig. 3). Species making up the 'Contaminants' and 'Stowaways' pathways were most frequently introduced specifically during the movement of commodities. Here, we found that species with the highest average cost were associated with indirect introductions following the release of species into the (semi)-natural environment: 'Aesthetic release', 'Agriculture' and 'Ornamental trade'. Over the last 50 years, 'Packing material' and 'Machinery & equipment' stowaways accounted for the highest costs (\$79bn and \$75bn, respectively). For intentional introduction pathways, species introduced through 'Pet trade', 'Other release' and 'Biological control' amassed the highest cost of \$50bn, \$47bn and \$45bn (**Supplementary Material 7**).

How are costs taxonomically and spatially distributed across pathways?

The costs of species introduced as 'Contaminants' and 'Stowaways' were mainly driven by insects, with a total cost of \$111bn and \$66bn, respectively. They were followed by mammals for 'Stowaways' (\$24bn) (e.g. *Rattus* spp.) and by plants for 'Contaminants' (\$18bn). Mammals drove the cost of species released into nature ('Release') or that have escaped ('Escape'), costing over \$50m between 1970 and 2020 (Fig. 4). Although most plant IAS were intentionally introduced and subsequently escaped, invasive plant species introduced as 'Contaminants' generated the greatest costs. There was no statistical difference in the total and average cost of plants introduced across pathways ($p > 0.05$).

The total cost each IAS pathway varied across regions. 'Stowaways' had the highest costs in Asia, Central America, North America and Diverse/Unspecified regions, whilst Antarctic-Subantarctic and Oceania incurred the greatest costs from species intentionally released into nature ('Release'). In Africa and Europe, 'Contaminants' generated the highest costs, followed by 'Escape' species (see Fig. 5). When considering the average cost of species for each pathway, 'Release' species were the most costly in Asia and South America, 'Contaminants' were the most costly in Africa, Europe, Oceania and Diverse/Unspecified region and 'Stowaways' cost the most in Central and North America (See **Supplementary Material 8**).

Are there differences in costs between species introduced intentionally and unintentionally?

The total cost of species introduced unintentionally is more than double the cost of species introduced intentionally (\$192bn vs. \$90bn respectively). The average species cost tended to be higher for species introduced unintentionally in terms of damage ($p = 0.085$), management ($p < 0.001$) and mixed costs ($p < 0.001$) than species introduced intentionally (Fig. 6a). Similar to this trend, over the period 1970–2020, species introduced unintentionally were found to cost more in terms of damage and management than species introduced intentionally (Fig. 6b) with unintentional introductions generating \$118bn and \$21bn in damage and management respectively versus \$78bn and \$10bn for species introduced intentionally.

When considering the different types of management costs (e.g. pre-invasion, post-invasion), unintentional introductions still generated more costs than intentional introductions (see **Supplementary Material 9**).

Is there a relationship between the number of introduction pathways and species cost?

There was a slight decreasing trend between costs of IAS and the number of pathways through which they are transported. However, we found no significant relationship between the total cost or the average cost of a species and the number of its pathways or pathway sub-categories (see Fig. 7).

Discussion

Using data from *InvaCost*, we set out to address four principal questions. First, we found that the average, as well as the total cost of species introduced through ‘Contaminants’ and ‘Stowaways’ were more costly than species introduced primarily through ‘Escape’ and ‘Release’, with ‘Unaided’ and ‘Corridor’ being the least costly. Second, this pattern varies spatially and across taxonomic groups, which should be taken into consideration when formulating policies. Third, the cost of species introduced unintentionally is more than double the cost of species introduced intentionally. Likewise, the average species cost also tends to be much higher for species introduced unintentionally in terms of damage, management and mixed costs than species introduced intentionally. Finally, unlike ecological impacts – where multiple pathways increase the likelihood of species’ having an impact (Pergl et al., 2017) – we found no relationship between the total and average cost of species and the number of pathways through which it is transported.

More than 40% of species with cost records had ‘Escape’ as a primary pathway of introduction making it the most common IAS pathway, followed by ‘Contaminants’ (24%), ‘Release’ (21%) and ‘Stowaways’ (16%). The proportion of species in relation to each pathway is in line with recent findings of McGrannachan et al. (2021). Although species introduced through ‘Escape’ and ‘Release’ are more numerous than species introduced as ‘Contaminants’ or ‘Stowaways’, their average and overall costs are significantly lower.

Such patterns can be attributed to a number of factors including species charisma, perceived utility and ease of management. IAS charisma – “characteristics that affect people’s perceptions, attitudes, and behaviors toward them” – can influence public support or contribute to social conflicts thereby affecting perceptions of costs and management actions (Jarić et al., 2020). As such, charismatic species are not only more likely to be introduced intentionally through, for example, the ornamental trade (van Kleunen et al. 2018) but are also more likely to receive social acceptance in the receiving region and generate public opposition to control measures (Jarić et al., 2020). This could lead to low reports of damage costs and paltry investment in management actions. For example, proposed controlled measures of the grey squirrel (*Sciurus carolinensis*) in the UK and Italy generated strong backlash from the public despite its

known impact on native red squirrel (*Sciurus vulgaris*) populations and potentially high economic damage cost (Bertolino and Genovesi 2003; Gurnell et al., 2004; Mayle and Broome, 2013). Moreover, intentional releases and escapes should in theory be more straightforward to monitor and control (Hulme et al., 2008) and therefore less costly. Although further evidence is needed to support this hypothesis, Pluess et al. (2012) suggest that eradication campaigns were more likely to succeed for plants introduced for cultivation and subsequently escaped, whilst fungi were the least likely to be eradicated, potentially due to their ability to spread and develop resistance to fungicides (Otten et al., 2004). Arguably, species introduced unintentionally may be able to spread undetected for longer, leading to greater economic costs compared to species introduced intentionally, for which one expects that better measures are already in place to prevent and control invasions.

In line with vertebrates being characterized as deliberate 'Releases' and invertebrates as 'Contaminants' (Hulme et al., 2008), mammals drive the total cost of intentional introductions (64%) whilst insects drive the total costs of unintentional introductions (67%). Indeed, charismatic and widely domesticated cats (*Felis catus*), wild boars (*Sus scrofa*) and rabbits (*Oryctolagus cuniculus*) represent 58% of intentional introduction costs. Their close proximity and value to humans either as game animals or as pets is a likely cause for their uncontrolled range and population expansion, consequently leading to extensive damage costs. On the other hand, insects are inconspicuous, so their sheer numbers and predominant impacts on sectors such as agriculture, health and forestry probably contribute to their high costs. The high reported costs of insects are the opposite of what we would expect if detection bias drove our results. When looking at the average cost per species, fungi and mammals, namely rats, stand out as the most costly 'Stowaway' species, and fungi and arthropods (other than insects) have the highest average species cost for 'Contaminants'. Indeed, rats are amongst the most impactful IAS as their costly effects are both global and multi-sectoral, pertaining to disease transmission, damage to infrastructures and social disruption among others (WHO 2019).

Interestingly, plants introduced through 'Release', 'Corridor' and 'Unaided' are more likely to have ecological impacts than those introduced as 'Contaminants' (Pergl et al., 2017). However, we found that the average and total cost of plants introduced as 'Contaminants' were higher compared to other pathways, despite more plant species being introduced intentionally. There were no statistical differences in costs of invasive plants across pathways. Pyšek et al. (2011) found that plants introduced deliberately have a higher establishment success rate than plants introduced unintentionally, although 'Contaminants' were as widely distributed as intentionally introduced species, and invaded a wider range of semi-natural habitats. This could explain the higher costs generated by 'Contaminants', despite the high number of 'Escape' plant species.

Some plants with the greatest associated costs were originally released through the aquarium trade or for aquatic horticulture (e.g. *Eichhornia crassipes*, *Hydrilla verticillate*, *Hydrocotyle ranunculoides*, *Lagarosiphon major*). Aquatic ecosystems are particularly susceptible to invasions due to their relatively high connectivity - both hydrological and organismal - through exchange of mobile species (including humans) that may spread plant propagules (Francis et al. 2019). Increased awareness of biosecurity

issues around the trade in aquatic plants is needed to help counter the future emergence of costly invasions (Champion et al. 2010), just as there has been increased recognition of the risks of fish introductions through this mechanism (Gertzen et al. 2008; Nunes et al. 2015; Lockwood et al., 2019). Furthermore, while the patterns and trends depicted here are based on only a subset of known IAS - i.e. those recorded in the *InvaCost* database, our results are aligned with previous findings in terms of proportion of IAS by pathways (Saul et al., 2017; McGrannachan et al., 2021). Hence, our study provides a sound basis for further improved pathway-based cost assessments for many more IAS.

Costs incurred as a result of unintentional introductions are the greatest globally and for most regions, except for Oceania and Antarctic-Subantarctic, where costs from 'Release' species have accrued the most over the last 50 years. With low levels of human activity in the Antarctic region, it is not surprising that cost records only relate to management measures of intentionally introduced mammals, even though both deliberate and accidental introductions have been reported (Frenot et al., 2005). Monetary quantification of damage from invasions may be more difficult when the impact is primarily environmental; especially since humans are perhaps more inclined to spend money to mitigate impacts that cause economic losses. The cost of deliberate introductions in Oceania highlights the importance of conducting impact assessments before intentionally introducing species into new environments. As an example, a number of species (e.g. rabbits, wild boars) have been deliberately released into (semi)-natural environments and caused massive impacts to both the environment and sectors of the Australian economy such as agriculture (Hoffmann and Broadhurst, 2016).

Given their high economic impacts, managing unintentional introduction pathways (i.e. 'Stowaway' and 'Contaminants') should be a priority for future biosecurity efforts, which must adapt to growing trends in global shipping (Sardain et al. 2019), and increased survivability of stowaways due to climate change (Pyke et al. 2008; Della Venezia et al. 2018; Kourantidou et al. 2015; Kaiser and Kourantidou 2021). Embracing emerging technologies for safer shipping such as eDNA detection techniques, recyclable plastic pallets (i.e. IKEA's OptiLedge), and the application of fouling-resistant paints to ship hulls will help meet these challenges (Callow & Callow 2011; Guan et al. 2019). At the level of international policy, agreements such as the Ballast Water Management (BWM) which finally entered into force in 2017 (close to 27 years after its initial design and 13 years after its adoption) (IMO, 2020) and the creation of global biofouling policy are instrumental to establishing a worldwide standard to mitigate stowaways on ship hulls (Davidson et al. 2016; Ojaveer et al. 2018; Galil et al. 2019). The upholding of existing international ballast water regulations, as well as improved ballast water management in Arctic regions, will be key in the face of warming arctic waters (Goldsmit et al. 2019; Kourantidou et al. 2015; Kaiser and Kourantidou 2021). Stricter enforcement of wood packing material protocols such as ISPM15 can help limit the transport of wood boring insects in wood pallets (Leung et al. 2014). Similarly, adopting a 'pest free status' (ISPM10) prior to the export of goods – especially through 'Aesthetic release', 'Agriculture' and 'Ornamental trade' – may help reduce costs associated with 'Contaminants' and 'Stowaways'. Interception of IAS by trained staff at ports of entries (airports, seaports) should also be a very efficient measure.

To conclude, using the most up-to-date compilation of monetary cost information on IAS we show that ‘Stowaways’ and ‘Contaminants’ (particularly stowaways in ‘Packing material’ and ‘Machinery & equipment’ and ‘Contaminant of plants’) cause the greatest economic impacts globally. Thus, prioritising measures to prevent and control unintentional species introductions is critical in order to reduce the overall economic burden of IAS. We also stress the importance of conducting impact assessments before deliberately introducing species into new environments and raising public awareness of the potential impacts of non-native species, especially those introduced through the pet and aquarium trade. Moreover, our findings stimulate the need for more and better cost assessments and their association with IAS pathways, as targeted management implemented to prevent IAS introduction is the most efficient way to limit further impacts to our ecosystems.

Declarations

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Authors’ contribution. AJT, CD and FC managed the project. All co-authors contributed to the design of the study. AJT, EJH, CB, PJH, MK and AN compiled the pathway dataset. AJT, CD, DM and RG checked the pathway dataset. AJT carried out the analyses and generated the graphical items with help from FC and input from all co-authors. AJT took the lead in writing the first draft of the paper with inputs from CD followed by all co-authors. All co-authors read and approved the final manuscript.

Conflict of interest. The authors have declared that no competing interests exist.

Data Resources. All data used in this study were made fully accessible as supplementary files (Supplementary file 1; Supplementary file 3; Supplementary file 4).

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Figures

Figure 1

Convention on Biological Diversity (CBD) pathway classification. Invasive alien species introduction pathway framework uses a hierarchical approach in which alien species may arrive in a new location through three broad mechanisms (i.e. movement of a commodity, arrival of a transport vector, or spread from a neighbouring region), 6 main pathways (i.e. release, escape, contaminant, stowaway, corridor, and unaided) and 44 pathway subcategories (e.g. ornamental, aquaculture, seed contaminant, etc.). Figure adapted from Hulme et al., 2008; CBD 2014 and Harrower et al., 2018.

Figure 2

Cost of species by introduction pathways. (a) Total cost of invasive alien species by pathway for the period (1970-2020) and (b) average cost per invasive alien species per pathway. Species can have multiple pathways although in this figure we only present ‘primary’ pathways of introduction that are likely to lead to successful long-distance introductions (see methods), which reduces the number of pathways per species. The width of the bars in (a) is equivalent to the number of species.

Figure 3

Average cost per invasive alien species by introduction pathway sub-category (1970-2020) (USD 2017 value). Species can have multiple pathways. Only 'primary' pathways of introduction are included in this figure. Boxes are coloured based on the main CBD pathway classification and ranked according to the median cost of species in each pathway sub-category.

Figure 4

Total cost of invasive alien species by introduction pathway and organism group (1970-2020) (USD 2017 value). Only 'primary' pathways of introduction are included in this figure. The colour of the bubbles represent the number of species recorded in InvaCost within each broad organism group and pathway and the size of the bubble represents the total cost of invasive alien species by broad organism group and pathway. For example, 'escape' from confinement is the primary pathway for 151 plant species and the total cost incurred for a plant introduced through 'escape' for the period 1970-2020 is \$ 1.2 billion.

Figure 5

Total cost of invasive alien species by introduction pathway and geographical region (1970-2020) (USD 2017 value). Only 'primary' pathways of introduction are included in this figure. The colour of the bubbles represent the number of species recorded in InvaCost for each region and pathway and the size of the bubble represents the total cost of invasive alien species by region and pathway. For example, 10 species recorded in InvaCost introduced primarily as contaminants in Africa cost a total of US\$ 6.8 billion over the period 1970-2020.

Figure 6

Cost of intentional and unintentional introductions by cost type (1970-2020)(USD 2017 value). Figure showing a) a boxplot of the average cost of species introduced intentionally and unintentionally by cost type and b) bar plot of the total cost of species introduced intentionally and unintentionally by cost type. Only 'primary' and 'direct' pathways of introduction are included in this figure.

Figure 7

Invasive alien species cost (1970-2020)(million USD 2017) against the number of introduction pathways. Both primary and secondary pathways are considered however only direct pathway subcategories are included in this figure. The colours represent the broad organism group each species belongs to.

Supplementary Files

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